

Higher-order cognitive processes moderate body tilt effects in vection

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ABSTRACT

Changing head orientation with respect to gravity changes the dynamic sensitivity of the otoliths to linear accelerations (gravitational and inertial). We explored whether varying head orientation and optic flow direction relative to gravity affects the perception of visually induced self-motion (vection) in two experiments. We confirmed that vertical optic flow produces stronger vection than horizontal optic flow in upright observers. We hypothesized that if this was due to aligning the simulated self-motion with gravity, then interaural (as opposed to spinal) axis motion while lying on the side would provide a similar vection advantage. Alternatively, motion along the spinal axis could enhance vection regardless of head orientation relative to gravity. Finally, we hypothesized that observer expectation and experience with upright locomotion would favour horizontal vection, especially when in upright posture.

In the first experiment, observers stood and lay supine, prone, left and right side down, while viewing a translating random dot pattern that simulated observer motion along the spinal or interaural axis. Vection magnitude estimates, onset, and duration were recorded. Aligning the optic flow direction with gravity enhanced vection in side-laying observers as reflected by either a bias for interaural rather than spinal flow or by an elimination/reduction of the spinal advantage compared to upright. However, when overlapping these signals was not possible—as in the supine and prone posture—spinal axis motion enhanced vection. Furthermore, perceived scene structure varied with head orientation (e.g., dots were seen as floating bubbles in some conditions).

To examine the influence of scene structure, in the second experiment we compared vection during simulated motion with respect to two environments: a rigid pipe structure that looked like a complex arrangement of plumbing pipes, and a field of dots. Interestingly, vertical optic flow with the pipes stimulus produced a similar experience to that of riding an elevator and tended to enhance vection.

Overall, we found that vection depended on the direction of both the head orientation and visual motion relative to gravity, but was also influenced by the perceived scene context. These findings suggest that, in addition to head tilt relative to gravity, higher-order cognitive processes play a key part in the perception of self-motion.

1. Introduction

The act of moving in an environment generates a pattern of optical flow that can indicate the direction and magnitude of self-motion. As well, a stationary observer viewing a similar flow pattern can experience compelling illusions of self-motion. This illusory percept of self-motion has been termed “vection” [1]. A common experience of vection is the “train illusion”, in which a passenger in a stationary train observes another train moving on an adjacent track and experiences a strong sense of self-motion in a direction opposite to the moving train. Determining self-motion depends on feedback from multiple sensory cues, including visual, vestibular, proprioceptive, tactile [2], and

interoceptive [3,4]. Of these self-motion senses, vision and the vestibular system play dominant roles.

In natural surroundings, it would be unusual for a stationary observer to see a large portion of their surroundings move [5]—i.e. to be presented with global optic flow. Accordingly, when a large segment of our visible surroundings are moving, we tend to attribute this motion to self-motion [6].

The vestibular system also signals self-motion. The otolith organs and semicircular canals sense linear and angular accelerations of the head, respectively [7]. In the case of an upright and translating observer, vertical self-translation is predominantly sensed by the saccules and horizontal translation by the utricles—though both are sensitive to

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motion in all directions [8–10]. Additionally, the vestibular organs are mechanical inertial sensors, and therefore cannot distinguish between being stationary and constant velocity motion [11–13].

Together, the visual and vestibular systems inform us about self-motion, and the direction of gravity—a constantly imposed acceleration [11,14]. The visual system is able to estimate the gravitational “up/down” by static and dynamic orientation cues, which are grounded in assumptions about the physical world—e.g., a tree trunk is rooted in the ground, and a tossed object falls toward the earth. Likewise, the otolith organs detect linear acceleration due to gravity, and hence signal the direction of gravity.

In most natural situations the visual and vestibular self-motion signals provide consistent information about the direction and magnitude of self-motion. Invection stimuli, the visual system signals motion while the vestibular system signals no motion and the occurrence, magnitude and time course of thevection percept are generally believed to reflect the resolution of this intersensory conflict (e.g. [15]). This intersensory integration is likely to depend on (1) the relative reliability of the senses, (2) the ambiguity of the signals, and (3) the ecological relevance and likelihood of the motion [6,16,17,15,18], all of which vary with the orientation of the stimuli with respect to gravity.

1.1. Differences in signal reliability: head-centric differences in otolith sensitivity

Many theories of multi-sensory integration propose that signals are combined according to their reliability. For example, maximum likelihood estimation combining commensurable and unbiased signals predicts weighting of cues proportional to their precision [19,20]. Similarly, Bayesian approaches model the precision of sensory signals in making a posteriori estimates and effective robust estimators need to discount unreliable signals [21,22]. In a cue-conflict situation such asvection, the strength of the percept should depend on the relative reliability/sensitivity of the visual and otolithic linear self-motion signals.

While the otoliths are each sensitive to head-centric linear acceleration stimuli in many directions, the anatomy of their respective maculae make the saccule more sensitive to vertical acceleration and the utricle to horizontal acceleration. Physiological, anatomical and psychophysical evidence also suggests that the human utricle is more sensitive than the saccule [23–27]. Some of the earlier studies of relative sensitivity only manipulated posture or used a single plane of motion and thus confounded head-centric and gravitational directions. MacNeilage et al. [26] systematically varied posture and motion direction and confirmed that sensitivity for motion detection and heading discrimination was lower for up–down (spinal axis) compared to left–right (interaural) motions. The direction of motion with respect to gravity did not affect sensitivity (although observers were generally less sensitive in recumbent posture).

Due to the head-centric nature of this directional vestibular sensitivity, duringvection stimuli the conflicting vestibular signal indicating no motion should be more reliable for horizontal than vertical motion [28,29]. In turn, based on this mechanism, vision should be weighted more heavily andvection should be stronger (larger magnitude, faster onset and longer duration) for spinal motion than interaural motion regardless of the orientation of the head¹.

¹Note that, as this discussion is based on relative cue reliability, similar considerations would hold if sensitivity to visual motion differed between vertical (spinally-directed) and horizontal (interaurally-directed) optic flow. Vertical and horizontal visual motion sensitivity have generally been reported as similar (e.g., [30]). Small anisotropies favouring horizontal motion have been reported for the visually-induced optokinetic response to optic flow [31] but, to be consistent with the uprightvection data, vertical visual motion should be favoured.

1.2. Ambiguity of the signals in our gravitational context

Accurately estimating self motion requires determining which components of the visual and vestibular signals indicate self motion. The distinction between object and self motion is an inherent ambiguity in the visual signal that was discussed above. The otolithic self-motion is also ambiguous as the otoliths detect all forms of self-acceleration including gravity. Thus the self-motion signal must be estimated from the ‘gravito-inertial acceleration (GIA) vector’—the sum of the acceleration vectors due to self-motion and gravity [32]. Conceptually, this extraction could be done by subtracting the gravity (1-g) vector from the GIA.

To perform such a vectorial subtraction the direction and magnitude of the 1-g gravitation signal need to be known. The instantaneous vestibular estimate of the GIA is ambiguous as the signal can result from various combinations of a 1-g signal orientation and motion directions and amplitudes. The problem is simplified if the head orientation relative to gravity can be determined (the perceptual upright). Evidence suggests that the perceptual upright is formed by combining visual, vestibular and other sensory signals to orientation with assumptions or priors such as the expectation that the head is generally upright [14,32,33].

When the gravity and self-motion vectors are parallel, the resulting gravito-inertial vector only changes in magnitude, but when self-acceleration is orthogonal to gravity it affects the direction and the magnitude of the gravito-inertial vector. Thus, if one moves vertically an earth-vertical acceleration signal would be added in the same direction as a larger gravitational acceleration [29]. There is evidence that human vestibular discrimination of self-translation obeys [34] or approximates [35] Weber’s law and thus should become less sensitive when loaded by gravity. This would predict strongervection in the direction of gravity, regardless of posture. Evidence of gravitational effects on self-motion were reported by [36], who found asymmetries and inversions in vertical linearvection when observers were in microgravity.

1.3. Ecological considerations

Our experience with moving through a constant 1-g environment has likely shaped the evolution and development of our perceptual systems. The saccular and utricular signal processing have evolved and developed to deal with a predominantly erect posture and thus a superimposed gravity signal and tilt sensitivity respectively. If the peripheral and central vestibular system has evolved to be optimized (tuned) for upright posture in 1-g environment then we might expect it to be less effective in other postures (e.g. as found in [26]) and, in turn,vection should be generally less restrained and thus stronger in lying compared to erect posture.

Our environment also determines the likelihood of the type of movements we make. Typically the sustained movements we make are mainly perpendicular to gravity except when climbing or falling. Thus extended periods of horizontal motion are more ecologically relevant than vertical motion. As discussed above, vestibular, visual and cognitive factors all influence the perception of upright. If directional biases invection depend on perceived orientation with respect to gravity then we may find they vary with the relative saliency of these factors in the stimulus.

Similarly, apart from special situations such as swimming, traveling while supine, prone or lying on one’s side are all unusual (i.e. non-ecological). Therefore, we might expect thatvection will be stronger when the observer is upright as opposed to lying down.

1.4. The role of posture with respect to gravity on linearvection

The role of posture with respect to gravity on linearvection sensitivity has received relatively little experimental attention. Kano [37]

reported that vection onset latencies were shorter for simulated up–down (spinal) motion than for forward/backward (naso-occipital) motion in upright observers (a finding replicated in [28]). However, in another experiment using supine observers, vection latency was shorter when the self-motion was perceived to be either towards the feet or gravitationally downward towards the back (compared to when self-motion was perceived to be toward the head or gravitationally upward towards the front). In contrast, while Guterman et al. [29] confirmed postural modulation of vection using a within-subjects design, they found that the effects of optic flow type direction (expanding versus contracting along the naso-occipital direction) remained relatively constant in various postures. In all these previous experiments, it is possible that any directional effects reflect the difference between the looming flow typical of forward/backward motion compared to the lamellar flow produced by vertical motion. To address this issue we note that lamellar flow can also be produced by lateral self motion, which could be compared more directly with vertical flow. To our knowledge, no one has studied the effects of posture on vection from lamellar flow either aligned with or orthogonal to gravity (but see [38] for experiments measuring heading perception in the coronal plane in various postures).

The factors outlined in Sections 1.1, 1.2, 1.3 suggest that vection should depend on the direction of motion with respect to the head and/or gravity. By varying motion direction we can make the direction of simulated self-motion congruent with or orthogonal to the gravity vector. By also varying posture we can dissociate the head centric and gravity centric directions of vection. Table 1 shows the relationship among postures, gravity, motion direction, and principal otolith sensitivity (see Fig. 1 for an illustration). Left-side and right-side down postures (roll tilt 90°) are interesting in that the roles of the utricle and saccule in sensing motion along the gravity axis are swapped compared to the erect posture. Conversely, in supine/prone posture, both the interaural and spinal axes are orthogonal to gravity. Several competing predictions can be formed about the relative potency of these stimuli in various postures based on potential mechanisms underlying the reported enhanced vection for spinal motion:

1. *Differences in otolith sensitivity, a head-centric mechanism.* If the saccule is less sensitive than the utricle then, during vection stimuli, the conflicting vestibular signal signalling no motion should be more reliable for horizontal than vertical motion. Thus, we hypothesize that vection will be stronger (larger magnitude, faster onset and longer duration) for spinal motion than interaural motion regardless of the orientation of the head.
2. *A direct gravity dependence.* If the spinal axis advantage for vection in

Table 1

A summary of the relationship between body-centric and gravito-centric frames of reference in different postures. Body axis convention was chosen to follow the computer graphics camera-space convention where z is in the view direction (thus the x-axis is interaural or left-right, y is spinal or up-down, and z is nasal-occipital or forward-backward). For each posture the table shows: (1) the direction of gravity in body-centric terms, (2) the gravito-centric direction of x-axis and y-axis directions of head motion and (3) the gravity sensitivity of the utricle and saccule. In the last two columns an asterisk indicates that the given macula is oriented for high sensitivity in the direction of gravity.

Posture	Gravity (relative to self)	Head-centric linear flow relative to gravity		Otolith sensitivity bias to gravity	
		Interaural (x-axis)	Spinal (y-axis)	Utricle	Saccule
Upright	y-axis	orthogonal	aligned	–	*
Supine/Prone	z-axis	Orthogonal	Orthogonal	–	–
Left/Right Side	x-axis	Aligned	Orthogonal	*	–

upright posture is related to directly to gravity (for example resulting from alignment of the motion with a large gravity signal) then the advantage should switch to the gravitationally-aligned interaural axis in roll and disappear in prone/supine postures.

3. *Specialization for locomotion over the ground plane in normal gravity.* If the peripheral and central vestibular system has evolved to be optimized (tuned) for upright posture then we might expect it to be less sensitive in other postures. In turn, vection should be generally less restrained and thus stronger in lying compared to erect posture.
4. *Cognitive/Ecological considerations.* Extended periods of horizontal motion are more ecologically relevant than vertical motion and thus horizontal vection should be easier to evoke than vertical vection. Visual, vestibular, and cognitive factors all influence the perception of upright and directional biases in vection may vary with the relative saliency of these factors in the stimulus. We also predict that vection will be stronger when the observer is upright as opposed to lying down as travelling while lying down is unusual.

In this paper, we show that vertical optic flow produces stronger vection than horizontal optic flow in upright observers. We also examined whether this effect is due to gravitational alignment or to alignment to the spine or trunk of the body. Observers viewed the same stimuli in various body orientations, including positions in which visual motion was along an axis in a plane that was orthogonal to gravity. In Experiment 1, we show that vection is influenced by both gravity-centric and body-centric direction. We then show in Experiment 2 that gravity and spinal effects in vection may be modulated by scene structure that influences the perceived context of a scene.

2. General methods

2.1. Subjects

Participants included eight observers (four males, four females; mean age = 30.88, SD = 9.96) in Experiment 1, and six observers (three males, three females; mean age = 26.5, SD = 3.56) in Experiment 2. All subjects had normal or corrected-to-normal vision and reported no vestibular impairment. Participants had prior experience with illusions of self-motion in a laboratory setting. Written informed consent was obtained in accordance with a protocol approved by the York University Research Ethics Board.

2.2. Apparatus

Subjects stood upright on stable foot blocks or lay on a foam mattress with a headrest to appropriately orient and center the head with a computer screen. The mattress enabled observers to maintain a full-body tilt of ±90° (left and right side down) about the naso-occipital (roll) axis, or to lay prone or supine. The stimuli were displayed on an IBM Lenovo T61p 15.4-in. TFT laptop with a resolution of 1280 (horizontal) × 800 (vertical) and refresh rate of 60 Hz. The laptop was mounted to a rigid frame with the screen frontal-parallel to the subject. Extraneous stimuli were masked using a circular viewing tube, cloth shroud, and a matt-black opaque aperture panel offset 1.5 cm from the screen. This aperture system set the observer-to-screen distance of 30 cm and the field of view of 39°. The aperture and viewing tube also promoted the sense of self-motion by (1) occluding extraneous peripheral stimuli and (2) providing a frame of reference for both relative motion and for perceiving the display as background - both stimulus factors have been shown to improve the vection induced by optic flow [39,40,18,41]. This provided the strong impression of looking through a window at the display beyond. This manipulation generated more compelling vection illusions, despite the relatively small central display.

Responses were recorded using a Logitech R Dual Action Gamepad (see Fig. 2). Subjects wore earplugs (model 1100, 3M) to mute

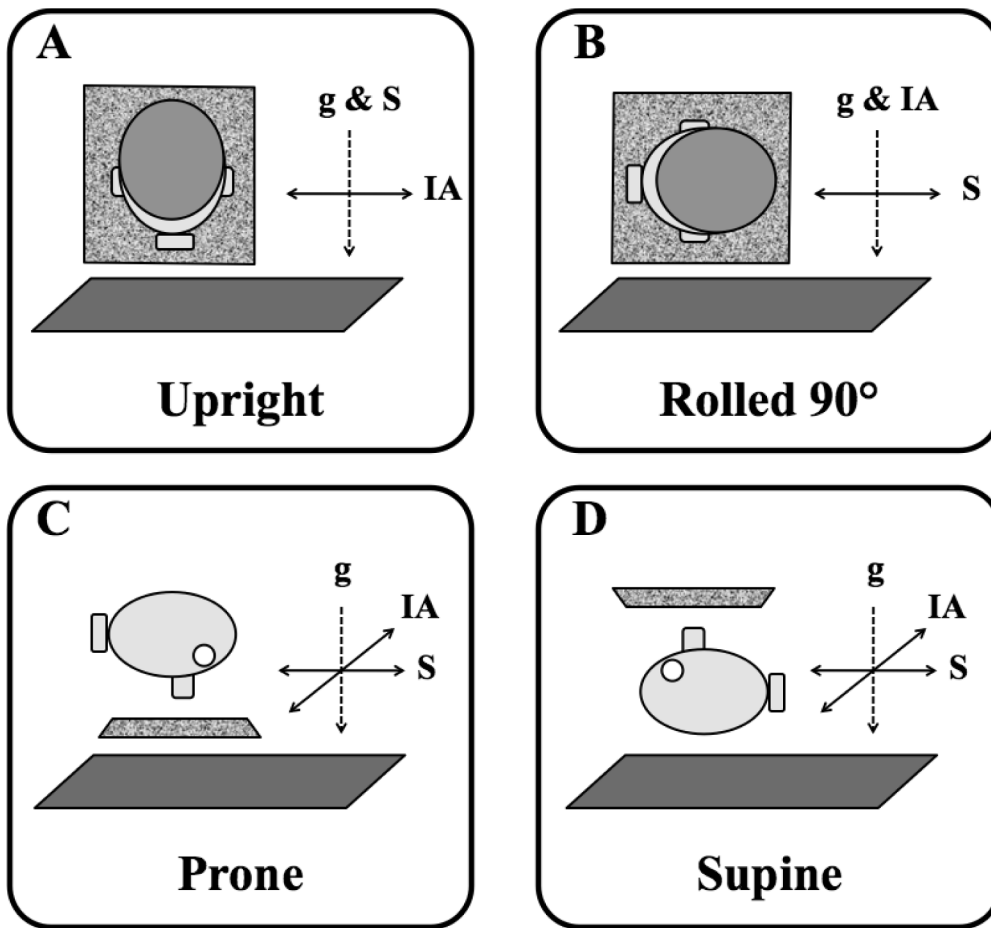


Fig. 1. Visual schematic of the spinal (S) and interaural (IA) stimuli directions relative to gravity (g), for the upright (A), tilted (B), prone (C), and supine (D) postures. The solid gray and textured polygons represent the ground plane and display, respectively. For each posture, visual motion was presented along the spinal or interaural axes. As shown above, the direction of the stimulus motion and gravity could be aligned when participants were upright (g & S) or roll-tilted (g & IA), but not when lying supine or prone.

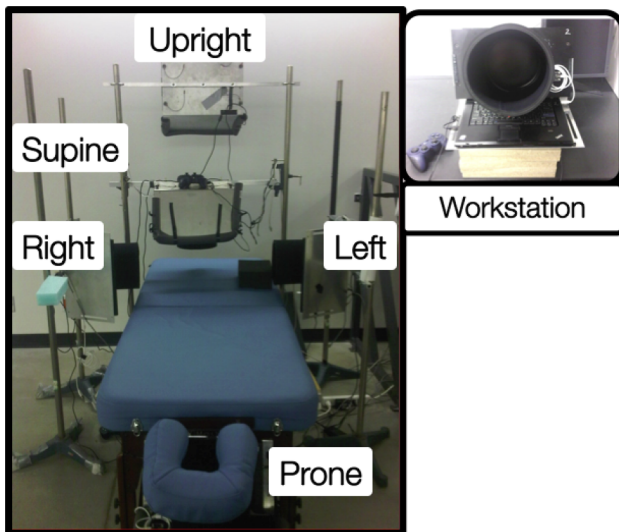


Fig. 2. Photograph of the apparatus for the upright (standing), tilted (lying on the left and right side), supine and prone postures. Foot blocks and a foam headrest were used for height adjustment and support.

extraneous auditory orientation cues.

2.3. Stimuli

The self-motion displays were generated using custom Python software with open-source Pyglet libraries (Experiment 1), Autodesk Maya and Adobe Media Encoder (Experiment 2). Stimuli were 3-D

animations (non-stereoscopic) of vertical and horizontal translation through a computer-generated scene. The virtual camera for the experiments had a vertical field of view of 39° to match the display.

In Experiment 1, the scenes consisted of a volumetric (3-D) optic flow field of 8500 randomly distributed blue dots (16.72 cd/m²) on a black background (0.64 cd/m²). The cloud of dots extended 30 m along the depth or visual axis. The dots had a simulated radius of 7.5 cm and were uniformly translated in 3-D space at 1.33 m/s to produce a lamellar flow pattern. The dots moved vertically or horizontally with respect to the display. When any dot moved beyond the field of view (off screen), it was redrawn at the same original vertical (or horizontal for vertical motion) and depth coordinates on the opposite side of the virtual scene. Stimulus duration was 30 s in Experiment 1.

In Experiment 2, the scenes contained the same 3-D dot scene as in Experiment 1, or a blue, rigid 3-D pipe structure of randomly distributed and intersecting virtual pipes in a volume of black space (see Fig. 3). The pipes were oriented vertically and horizontally with respect to the display. Self-motion was simulated by translating a virtual camera through the pipe structure. The rendered animation frames were rotated to produce the stimuli for both the vertical and horizontal translation. Stimulus duration was 20 s. The motion sequences were rendered with a frame rate of 30 frames per second as in Experiment 1, and the translation speed was 1.33 m/s.

2.4. Posture conditioning

While viewing the displays in the upright and lying postures, the head was aligned with the trunk of the body and the legs were extended. Only in the upright, left and right side down postures, was one of either the spinal or interaural body axes aligned with the direction of gravity; these body axes were orthogonal to gravity in the supine or

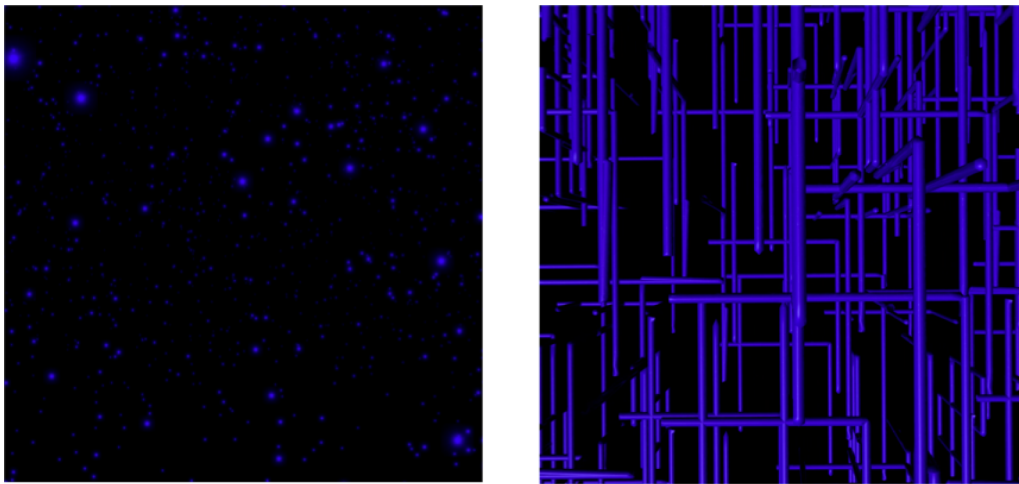


Fig. 3. Screenshots of the dot (A) and pipe (B) stimuli. Camera motion through these scenes was upward, downward, leftward or rightward depending on the condition.

prone postures. Fig. 1 shows the direction of the body axes relative to the direction of gravity. The trials began after approximately 60 s in the given posture.

2.5. Procedure

The procedure was similar for the two experiments. Observers viewed a series of self-motion displays while casually looking about the display and attending to their perception of self-motion. In Experiment 1, observers first tested in the standing posture followed by testing in lying postures, which included lying left and right side down, supine and prone. In each session, they first stood upright and viewed a 30 s lamellar dot motion display (vertical or horizontal motion as appropriate for the block) while attending to their sensation of self-motion. Observers were told to assign a vection magnitude of 50 to the vection sensation produced, which served as a reference stimulus for subsequent trials.

During each trial, observers viewed the dot displays and pressed one of the shoulder buttons on a gamepad as soon as they experienced vection, and continued to hold the button until that sensation or trial ended. If vection ceased and reoccurred during a trial, the shoulder button was to be pressed again. Each trial was followed by a response screen prompting observers to use the gamepad to indicate their overall sensation of self-motion on a rating scale of 0–100 relative to the reference stimulus. The rating scale had a resolution of 5 units. If the observer's feeling of self-motion was twice as strong (or more) than the reference stimulus, they were told to give a rating of 100. If observers did not experience self-motion, they were asked to provide a rating of 0.

In Experiment 2, observers stood and lay left side down, while viewing 20 s lamellar motion displays consisting of either the same dot motion as in Experiment 1, or motion across a scene of pipes. Each display was followed by a black, blank screen, during which observers verbally reported their sensation of self-motion on a rating scale of 0–100. Observers were told to give a rating of 100 for maximal/saturated vection (i.e., they perceived themselves as moving in a world of stationary dots/pipes), and 0 if they did not experience vection (i.e., they perceived themselves as stationary with dots or the pipe structure moving past them).

For each trial, the motion direction (vertical or horizontal) and stimulus type (dots or pipes for Experiment 2) were randomly selected and blocked by posture. Within each posture block, trials were randomly ordered. The blocks were ordered using a counterbalanced design.

Qualitative reports of observers' vection experiences were collected during the experiment debriefing. Participants were asked the open-

ended question “How would you describe your experience of self-motion?” to potentially reveal any unintended or unexpected perceptions or sensations during or following the experiment.

2.6. Data analysis

Linear mixed effect model data analyses were performed using the R package nlme [42] with RStudio. Outlying points were identified through regression diagnostics (using the function `influence.measures` in R) confirmed with visual inspection of the response measures. Points were excluded based on (1) DFFIT which identifies an influential outlying data point based on the difference between the fitted values for the data point in the full dataset compared to the fitted value after deleting the data point [43,44] and (2) the covratio which estimates the change in the covariance matrices for the fixed effects if an observation is deleted [45,46]. We confirmed that results were qualitatively similar if these outlying points were included in the analysis.

We adopted backward stepwise selection based on Akaike's Information Criterion (AIC) to select the final regression models. Separate statistical models were fitted for each of the response measures, which were vection onset, duration, magnitude (Experiment 1 only) and saturation (Experiment 2 only). A goodness-of-fit test based on the analysis of deviance was used to evaluate the fit the model. Planned comparisons for the main hypothesis of spinal versus interaural vection differences were run using linear contrast tests of the models. Family-wise error was controlled for with Bonferroni-Holm correction and the adjusted p-values are shown for post hoc analyses. Trials in which vection was not reported were excluded from the analysis. Effect sizes for the linear mixed effect model parameters were computed as f^2 as described in Selya et al. [47].

3. Experiment 1

In the first experiment, we examined whether the relative alignment of the direction of head tilt and simulated self-motion modulates vection. We dissociated these body and display vectors from gravity by varying body posture with respect to gravity. In the upright posture, the display-vertical (and spinal axis) was aligned with the direction of gravity. In contrast, in the on-side conditions the interaural axis was aligned with gravity. As shown in Fig. 1, the visual motion and gravity do not align at all in the prone and supine posture.

3.1. Methods

There were three independent variables Reference (4 levels: up,

down, left, right), Posture (5 levels: upright, left side down, right side down, supine and prone), and stimulus Direction (4 levels: up, down, left, right, relative to the display). Trials were sessioned and blocked by the direction of the reference stimulus, and within these reference blocks blocked further by posture (20 blocks of 4 Ref. x 5 postures). Prior to a testing block, subjects stood and viewed a reference stimulus moving in one of the four motion directions (up, down, left, and right). They then moved to the appropriate posture for the first block and viewed one test stimulus for each of the four motion directions. After each trial, they rated their vection relative to the reference stimulus. After these four trials, they moved to the posture for the next block.

3.2. Results and discussion

Vection was reported for nearly all of the trials (approximately 97% of the total responses, comparable to other recent studies [48]). Data points that were identified as outlying or where vection was not obtained were removed included 33 data points (across response measures). To confirm that removing this data did not affect the outcome, we also repeated the analysis assuming the limits of the stimulus (e.g. onset latency of 30 and duration of 0 s) and the pattern of results was unchanged.

Fig. 4 shows the vection ratings averaged across all subjects. As

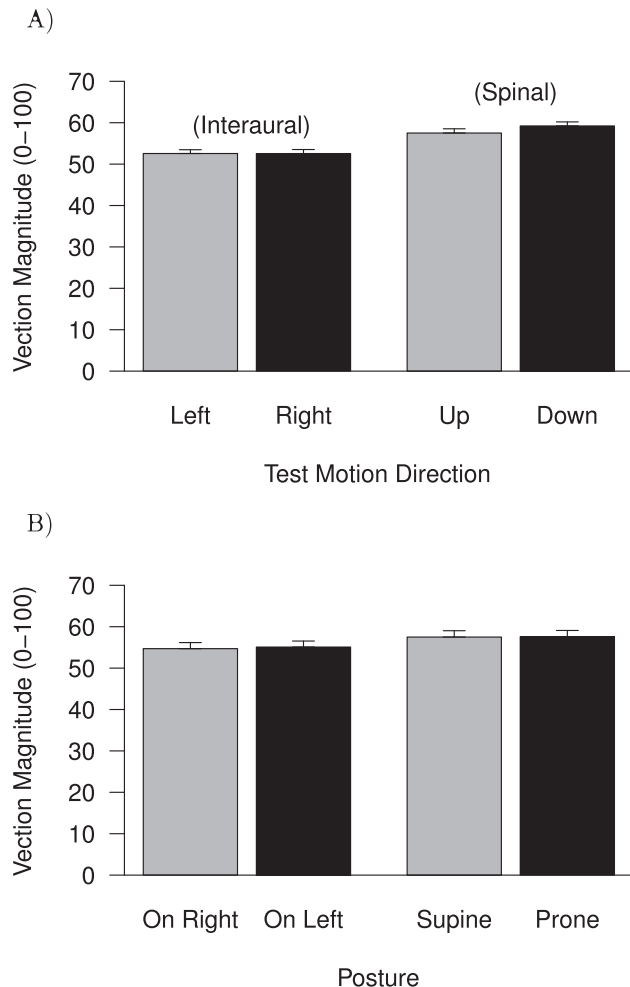


Fig. 4. Mean vection magnitude ratings (± 1 standard error of the mean (SEM), 8 observers) for (A) opposing motion directions across postures, and (B) opposing body tilts. Ratings for both types of opposing conditions were not significantly different (p 's $> .05$). Observers based their magnitude estimates on a reference stimulus with a given vection rating of 50, corresponding to one of the four reference motion directions before each block of trials.

shown in Fig. 4A, there were no significant vection differences between the opposing motion directions for vertical (up/down) or horizontal (left/right) motion for the reference and stimulus directions (p 's $> .05$), so these levels were collapsed into the two head-centric reference directions "Interaural" and "Spinal." There were also no significant differences between laying left and right side down (p 's $> .05$), or supine and prone (p 's $> .05$), so these conditions were combined and noted as "Rolled 90°" and "Pitched 90°" postures, respectively (see Fig. 4B). The results shown in subsequent figures are from data collapsed across these motion directions and postures.

Following this grouping of levels, the experimental design consisted of the following three factors: Reference (4 levels: up, down, left, right), Posture (3 levels: upright, rolled 90° and pitched 90°), and stimulus Direction (2 levels: interaural and spinal). Model selection began with the fully factorial model with subject as a random factor (models expressed in Wilkinson notation [49]):

$$\text{measure} \sim \text{posture} * \text{direction} * \text{reference} + (1|\text{subject}).$$

The model selection process attempted to produce simpler models based on the AIC. This resulted in a model for the three measures that was used for further analysis:

$$\text{rating} \sim \text{posture} * \text{direction} + (1|\text{subject})$$

$$\text{onset} \sim \text{posture} * \text{direction} + (1|\text{subject})$$

$$\text{duration} \sim \text{posture} * \text{direction} + (1|\text{subject})$$

Consistent with predictions, visual motion that was aligned with gravity enhanced vection. However, when the motion axis was orthogonal with gravity (in the pitched postures), motion along the spinal axis resulted in more compelling vection than interaural motion. Figs. 5–7 show the mean vection ratings, onsets, and durations across all subjects. Specifically, body orientation significantly influenced vection ratings, $F(2, 947) = 10.33, p < .0001, f^2 = 0.007$; onset, $F(2, 947) = 3.31, p = .0370, f^2 = 0.019$; and duration, $F(2, 947) = 11.04, p < .0001, f^2 = 0.073$. Vection durations were larger and onsets shorter in upright compared to lying posture (upright-roll duration $t(7) = 8.09, p = .0005$; upright-pitched 90° duration $t(7) = 4.43, p = .0150$; upright-roll onset $t(7) = -3.80, p = .0268$; upright-pitched 90° onset was marginal $t(7) = -2.94, p = .0655$). The test motion axis also had a significant impact on vection ratings, $F(1, 947) = 64.51, p < .0001, f^2 = 0.044$; onset, $F(1, 947) = 4.57, p = .0328, f^2 = 0.007$; and duration, $F(1, 947) = 12.16, p = .0005, f^2 = 0.014$. While there was a significant posture x motion axis interaction for observer vection ratings, $F(2, 947) = 16.42, p < 0.0001, f^2 = .035$, this was not the case for vection onsets or durations (p 's $> .05$).

In directly comparing interaural and spinal motion by posture, we found that when observers were upright, vection ratings and durations were significantly higher for visual motion that was presented along the spinal axis compared to interaural motion (ratings: $t(7) = 8.06, p < .0001, d_m = .85$; durations: $t(7) = 3.50, p = .0100, d_m = .16$) but while onsets were also shorter the difference was not significant ($t(7) = -2.14, p = .0692, d_m = .06$). In contrast, when observers lay on the side (rolled 90°), interaural motion did not produce significantly stronger vection than spinal motion (neither larger ratings, shorter onsets nor longer durations, all p 's $> .05$). While not significant, the interaural motion produced larger average vection ratings than spinal motion when observers lay on the side, suggesting if anything the effect had switched to interaural enhancement. However, when observers were supine or prone (pitched 90°), visual motion along the spinal axis resulted in significantly higher vection ratings ($t(7) = 3.02, p = .0192, d_m = .31$) and marginally longer duration ($t(7) = 2.21, p = .0630, d_m = .13$), with no significant difference in vection onset ($t(7) = -1.59, p = .1554, d_m = .07$).

Our finding that the relative direction of the body and visual motion axis significantly influenced vection, is consistent with that of previous

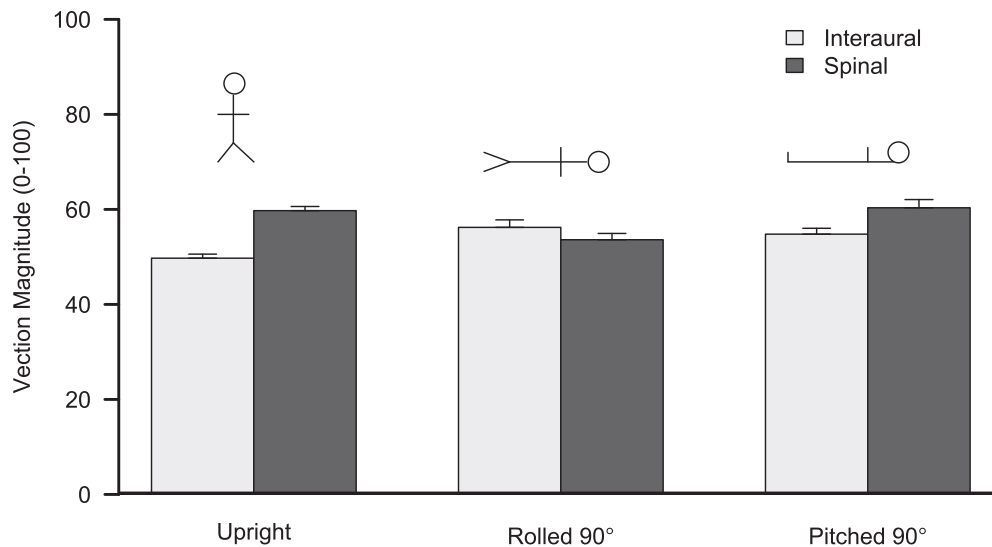


Fig. 5. Mean vection magnitude ratings for the upright posture (Experiment 1, far left) compared with the tilted, prone, and supine postures (± 1 SEM, 8 observers). Ratings for the opposing motion directions for vertical (up/down) and horizontal (left/right) test and reference stimuli were not significantly different ($p > .05$) and so were collapsed and coded into the two head-centric reference frames Interaural and Spinal. The vection magnitude ratings for the left and right side down, and supine and prone postures, were also not significantly different ($p > .05$) and so were collapsed into the “Rolled” and “Pitched” body orientation conditions.

vection studies in which these factors enhanced the feeling of illusory self-motion in observers [28,37]. However, consider that in the upright posture, the head-centric vertical/up was the same as gravity, so it is unclear whether the vection advantage for vertical motion with respect to the display was due to alignment with the spinal axis or the gravity axis. Thus, from the data for the upright posture, it may be argued that (a) gravity reinforced the visual signal in vertical vection, (b) there is a preference for motion along the trunk of the body, or (c) both the gravity and body vectors influence vection. The results from the rolled and pitched postures suggest that the latter conclusion is most correct, that both gravity and body influence vection. In other words, the strength of visually-induced self-motion depends on the axis of visual motion relative to both gravity and the body. In particular, this is evident in (1) our finding that in roll-tilted observers vection was relatively enhanced for interaural motion eliminating the spinal advantage found in upright observers, (2) preservation of the spinal motion advantage for pitched observers. This pattern was found for all of the response measures, but to a lesser degree for vection onset and

duration than magnitude.

The similarity of responses for vection from flow in opposing motion directions (vertical up/down and horizontal left/right), suggests that these alignment effects are not due to a simple vector summation of the visual and gravity signals. Furthermore, the lack of a significant vection difference between the supine and prone postures is consistent with the similar pressure sensitivities of the chest and back of the body [50].

During the session debriefing, three observers spontaneously reported that when they were roll-tilted, the stimulus motion appeared to be moving along a tilted axis with respect to the vertical and horizontal axis of the display—a possible A-effect (for a review see [51–53]). One of these observers also reported illusory scene shearing/distortion during the perceived self-motion.

Additionally, some observers reported that the dots stimulus looked like stars and that this resulted in sensations of flying through outer space. For other observers, the dots sometimes appeared as moving bubbles or snowfall, and this created the impression that they were stationary and viewing a moving stimulus, or more commonly moving

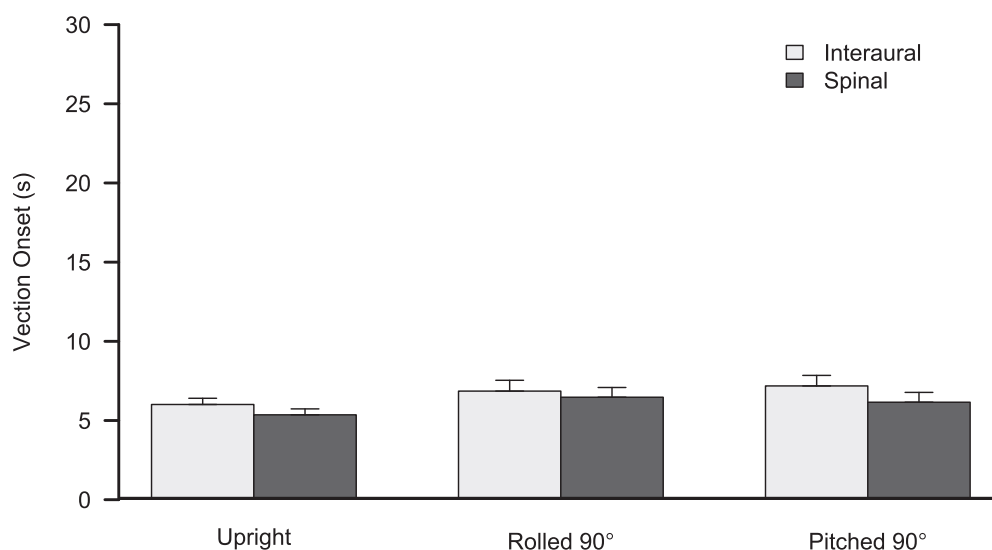


Fig. 6. Mean vection onset (± 1 SEM, 8 observers). Onsets for the opposing motion directions for vertical (up/down) and horizontal (left/right) motion were collapsed into the head-centric axis directions Interaural and Spinal.

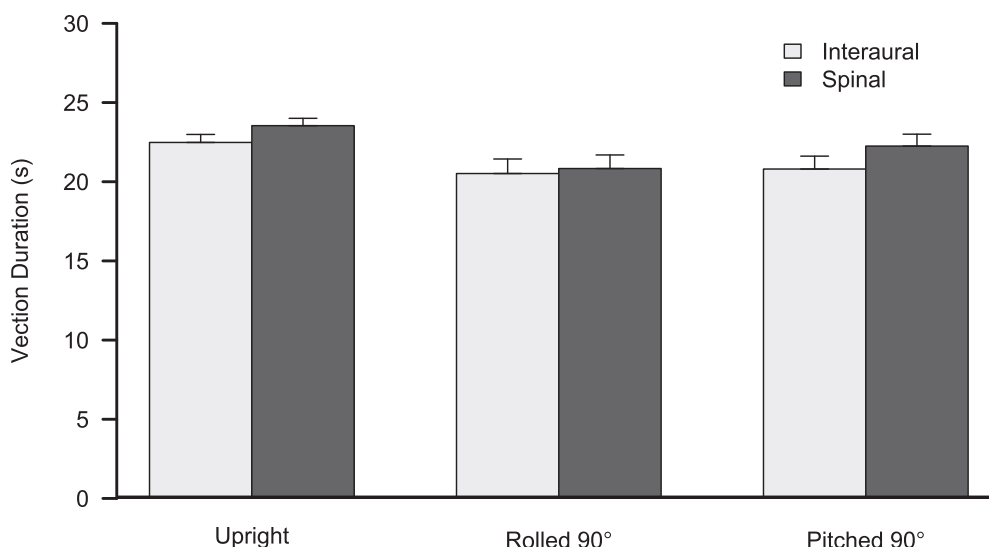


Fig. 7. Mean vection duration (± 1 SEM, 8 observers). Durations for the opposing motion directions for vertical (up/down) and horizontal (left/right) motion were collapsed into the head-centric stimulus axis directions Interaural and Spinal.

through elements that are also moving.

The fact that vection can be incomplete or dropout during the optic flow stimulus and produce object motion percepts are well-known phenomena (for review see [11]). The interesting observation here is that the interpretation of the object motion percept during unsaturated vection appeared to vary with posture. That is, that the object motion in the same stimulus could be perceived in different ways depending on posture and motion direction. As these phenomena were brought to light during the debrief, it was unclear as to the role that the perceived scene context or scene structure might have in influencing the effects of motion-gravity alignment in vection.

4. Experiment 2

While much of the research on self-motion perception has taken a “bottom-up” approach and focused on the roles of the visual and vestibular system [54,15,55], vection and other self-motion studies using virtual reality have demonstrated that cognitive or “top-down” mechanisms can affect the intensity, onset, and realism, of visually-induced self-motion. Accordingly, [56] used a flight simulator simulating linear and circular self-motion and found that vection saturation was enhanced when the motion in the scene was more naturalistic. Similarly, Riecke et al. [6] presented observers with naturalistic (coherent and incoherent/scrambled) and unnaturalistic 3D scenes of simulated self-motion using a dome projection setup, and found that scenes that were both coherent and naturalistic enhanced vection and “convincingness” of the illusory sensation of self-motion. Riecke et al. posited that such scenes provide the viewer the impression of a more stable visual environment, and thus the visual motion is more likely to be attributed to self-motion than external motion.

In the second experiment, we examined whether the influence of body orientation and motion direction with respect to gravity might depend on scene structure. To explore how the structure of a scene influences the perception of self-motion, observer posture was varied relative to gravity while they viewed motion along the spinal and interaural axis. The displays simulated self-motion across a 3-D volume of dots as in Experiment 1, or a 3-D scene that contained a single, solid pipe-like structure; we refer to these stimuli as “dots” and “pipes” respectively.

4.1. Methods

The procedure was the same as Experiment 1, except observers

viewed lamellar global optic flow displays while standing upright and lying down. There were three independent variables: (1) Body posture: standing (upright) and lying left side down (roll-tilted 90°); (2) Simulated self-motion direction: up, down, left, and right (relative to the display); and (3) Scene type: dots and pipes. Trials were divided into two blocks by posture, to limit the number of postural changes required given the four motion directions and differently-structured stimuli. For each of the two postures, the 8 factorial combinations (4 motion directions \times 2 scene types) were repeated 4 times for a total of 32 trials per block an overall total of 64 trials per subject. For each trial, we recorded the vection saturation (rating of 0–100). A vection saturation response of 0 meant the scene was perceived as moving and the self as fully stationary, and 100 meant that the scene was perceived as stationary and the self as fully moving.

4.2. Results and discussion

Fig. 8 shows the mean vection ratings across subjects. There were no

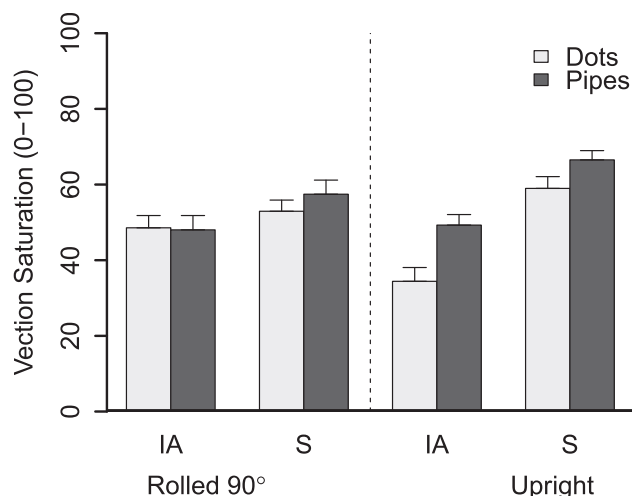


Fig. 8. Mean vection saturation rating (± 1 SEM, 6 observers). Ratings for the opposing motion directions for vertical (up/down) and horizontal (left/right) motion were not significantly different ($p > .05$) and so were collapsed into two motion directions (vertical and horizontal) and coded into the head-centric reference frames Interaural and Spinal. Here, the “Rolled 90” posture represents the left side down body orientation.

significant differences between the opposing motion directions for vertical (up/down) or horizontal (left/right) motion, so these levels were collapsed into the two head-centric motion directions Interaural and Spinal.

Using this two-level direction factor, the model selection began with the fully factorial model with subject as random factor:

$$\text{rating} \sim \text{posture} * \text{direction} * \text{sceneType} + (1|\text{subject}).$$

The model selection process attempted to produce simpler models based on the AIC. This resulted in a model without the non-significant three-way interaction that was used for further analysis:

$$\begin{aligned} \text{rating} \sim & \text{posture} + \text{direction} + \text{sceneType} + \text{posture: direction} \\ & + \text{posture: sceneType} + \text{direction: sceneType} + (1|\text{subject}). \end{aligned}$$

As in Experiment 1, body orientation had a significant effect on vection, $F(1, 367) = 10.50$, $p = .0013$, $f^2 = .0002$, and so did the direction of visual motion, $F(1, 367) = 4.29$, $p = .0390$, $f^2 = .1237$. The scene/stimulus type (dots or pipes) did not have a significant main effect on vection, $F(1, 367) = 0.43$, $p = .5090$, $f^2 = .0265$; however, interactions indicated that the effect of stimulus type depended significantly on body orientation, $F(1, 367) = 5.32$, $p = .0217$, $f^2 = .0139$, but not on visual motion direction ($p = .76$, $f^2 = .0002$). There was also an interaction between body orientation and motion direction, $F(1, 367) = 12.84$, $p = .0004$, $f^2 = .0345$. As in the first experiment spinal motion produced significantly stronger vection in upright observers $t(5) = 7.46$, $p = .0027$, $d_{rm} = .95$; however, in tilted observers, there was no significant difference in vection between interaural and spinal motion, $p > .05$, but rather, a trend towards stronger vection for motion along the spinal axis. Thus, consistent with experiment 1, there was a significant vection advantage for spinal motion in erect observers but when the interaural axis was aligned with gravity by lying on the side there were no significant differences in vection between interaural and spinal motion.

Additionally, upright observers experienced stronger vection when viewing the pipes than the dots ($t(5) = 3.89$, $p = .0115$, $d_{rm} = .46$). When participants were roll-tilted left side down, vection strength for the dots and pipes stimuli were not significantly different ($t(5) = 0.59$, $p = .5787$, $d_{rm} = 0.07$).

Interestingly, in the debriefing observers reported that the pipes stimulus gave the impression of being in a moving elevator and this effect tended to enhance vection; however, this “elevator effect” was reduced when observers lay tilted, as some felt that this effect seemed less natural when they lay on the side given the atypical posture for that perceived context. Therefore, the perceived context and naturalness of the scene had the potential to both enhance and inhibit vection. Such observer anecdotes demonstrate the effects of scene interpretation on illusory self-motion, and suggest that higher-order cognitive processes may be involved in vection.

5. General discussion

Varying head orientation allowed us to partially dissociate the effects of the direction of gravity with respect to the head, visual motion direction, and otolith sensitivity, on vection. Varying posture has been shown to modulate experiences of visually-induced self-motion [37,29] and we confirmed this in the present study. In the Introduction, we discussed potential mechanisms that could underlie a postural modulation of linear vection based on vestibular (otolith) sensitivity, resolving ambiguity in the context of a 1-g environment, and ecological considerations including specialization for locomotion over the ground plane and the role of expectations.

5.1. Differences in signal reliability: head-centric differences in otolith sensitivity

Anisotropies in the sensitivity of the otolithic system to linear acceleration predict head-centric biases in linear vection. As the utricle is generally considered more sensitive than the saccule to translation [23–27] we expected the otolithic conflict to be stronger and thus the vection sensation weaker for interaural compared to spinal vection, regardless of posture. We confirmed that this anisotropy held for erect observers. Based on similar logic, Giannopulu and Lepecq [28] predicted and confirmed that vection along the naso-occipital axis (sensed more by the utricle) would generate greater sensory conflict and thus longer onset latency than vection along the spinal axis (where the saccular response predominates) in erect observers. However, in [28] the optic flow differed in the two conditions with the naso-occipital flow being mainly looming flow and the vertical translation producing lamellar flow. Our flow conditions were both lamellar thus we can attribute the enhanced vection for spinal motion to the direction of simulated motion rather than the flow pattern produced.

Importantly, this hypothesis predicts that the anisotropy will be determined by the head-centric direction of simulated self-motion regardless of posture. We have evidence for this head-centric dependence in our supine and prone conditions in Experiment 1 where, as in upright posture, spinal flow produced significantly stronger vection (larger magnitude, shorter onset and longer duration) than interaural flow. In these pitched 90° conditions gravity is orthogonal to the motion and thus we expect that any head-centric dependence would not be affected by gravity. Anisotropies in sensitivity for vestibular motion detection and vestibular heading discrimination show an analogous head-centric dependence regardless of posture [26] consistent with the hypothesis that vection anisotropy reflects the reliability of the conflicting vestibular cue. Interestingly, the same study found no head-centric dependence of visual heading judgements. This is interesting since there is significant evidence for optimal visual-vestibular cue integration (in an either an MLE or Bayesian sense) that would predict performance would reflect the reliability of the underlying vestibular cue [57–61]. It is likely that visual heading direction discrimination and vection reflect different vestibular-visual integration processes (see [16] for discussion) and this may explain why our vection results reflect the anisotropy in vestibular motion sensitivity while the visual heading results [26] do not.

5.2. Ambiguity of the signals in our gravitational context

A pure head-centric difference in sensitivity as discussed in the previous section cannot be the entire story as the spinal versus interaural anisotropy diminished or reversed in the on-side postures in Experiments 1 and 2. This suggests a gravity dependence as well as a head-centric anisotropy, consistent with previous studies [29,36,37].

In upright posture, both head-centric and world/gravity-centric frames are aligned and so we cannot dissociate the role of these factors. Side-lying postures make these components orthogonal (see Table 1). If the anisotropy found in upright posture were a purely gravitational effect then we would expect a full reversal of the anisotropy when rolled 90° and a significant enhancement for interaural compared to spinal motion. In both Experiment 1 and 2, adopting the roll postures reduced or eliminated the spinal advantage consistent with a relative enhancement of the interaural axis stimulus that was aligned with gravity. However, in neither experiment was there a full reversal of the effect. Any remaining anisotropy in on-side posture was much smaller than the spinal advantage in upright observers. Thus, while we have evidence that alignment with gravity modulated the directional anisotropy it cannot fully explain it. Combined with our clear evidence for a spinal advantage in pitched 90° postures, the most parsimonious interpretation is that both gravitational and body centric factors play an important role in the perception of self-motion. Similar conclusions

were reached by Kano [37] for forward and vertical vection and by Bourrelly et al. [62] for heading estimation in pitched observers, respectively. In our experiments, head-centric and gravito-centric factors appeared to reinforce each other in upright posture providing a strong spinal advantage but approximately balanced each other in on-side postures nulling this advantage.

One possible factor underlying the gravitational dependence in our results could be the fact that gravitationally vertical motions must be interpreted in the context of a large and omnipresent 1-g gravity signal. Thus, signal-noise ratios should be significantly different for gravitationally vertical compared to horizontal self-motion. Human vestibular discrimination thresholds for self-translation increase with stimulus intensity [34,35] and thus the vestibular system should become less sensitive when loaded by gravity (the gravity-pedestal hypothesis). This reduced sensitivity predicts stronger vection along the direction of gravity, regardless of posture. However, McNeilage et al. [26] found that vestibular thresholds did not depend on orientation to gravity which is inconsistent with the hypothesis that a gravitational-pedestal reduces sensitivity—remarkably the vestibular system seems to maintain sensitivity in the presence of a 1-g pedestal [35]. Achieving such gravity-independence requires that the self-motion system estimate and compensate for the 1-g signal and this compensation process may underlie the gravitational sensitivity of vection even it is not reflected in vestibular sensitivity. An omnipresent 1-g signal leads to a tilt-translation ambiguity in the interpretation of changes in otolith signals (e.g., [63,64]) and to qualitative differences in the signals for vertical and horizontal motion [63,65]. Detection of horizontal motion with respect to gravity depends on discrimination of the orientation of the resulting gravito-inertial vector whereas detection of vertical motion requires estimating changes in its magnitude.

Related to this 1-g pedestal effect is potential for up-down asymmetries [66,67,24,35]. Unlike Seya et al. [68] who reported larger vection ratings for self-motion downward toward the feet than upward toward the head, we found no up-down biases—in either head-centric or world-centric coordinates—for vection ratings, onset latencies or duration. Our findings are consistent with other vection studies [18,69,70] and with other reports of no up-down asymmetry in vestibular sensitivity [26,71].

5.3. Specialization for locomotion over the ground plane in normal gravity

Self-motion sensitivity to head tilt was examined by [72] who found that tilting the head during roll or pitch vection stimuli enhanced visually-induced sensations of self-pitch and roll. They attributed this to reduced otolith sensitivity [73,74], and hence reduced cue conflict restraining vection, due to a less sensitive orientation of the macular planes relative to gravity. For linear motion, MacNeilage et al. [26] reported that vestibular sensitivity was generally reduced in on-side lying compared to upright posture. Thus in the present experiments, if tilting or pitching the head with respect to gravity makes the vestibular system less effective, then we would have expected increased vection when lying down due to the reduced cue conflict. However, consistent with prior studies [37,29], the erect posture produced vection with longer durations and shorter onsets than the lying postures. Interestingly, [26] reported that visual heading judgements were also less precise when tilted on side compared to upright posture (but [38] found no differences between supine and upright posture). These effects of tilt suggest a more general effect of posture reflecting that the combined self-motion system (rather than only the vestibular component) might be particularly tuned for self-motion in upright individuals.

5.4. Ecological and cognitive considerations

Here, we have demonstrated that the perception of self-motion can be influenced by the alignment of visual motion with both gravity and the body, and is also dependent on the perceived context of the scene.

These findings may reflect ecological considerations as well as low-level sensory sensitivity differences. Typically the sustained movements we make are mainly perpendicular to gravity except when climbing or falling. Since vestibular, visual and cognitive factors all influence the perception of upright it is perhaps not surprising that these factors all influence vertical-horizontal anisotropies in vection. The vection advantage for lamellar motion along the spinal axis when in supine and prone postures, may be because in an upright observer, this axis would also be along the “up/down” direction of the body. The body is typically aligned (during real locomotion) with both the visual and gravitational up and we evolved to deal with this predominantly upright posture for self-motion. Our prediction that horizontal vection should be favoured over vertical vection based on ecological relevance was not supported. This ecological view is consistent with our finding that vection had longer duration in upright posture compared to in lying postures (where such self-motion is unlikely) although the effects were modest. These types of ecological considerations could be incorporated in cue combination models, for instance by determining appropriate priors for Bayesian visual-vestibular cue integration models [57,58,60,61]. However, our finding that the perceived context of the visual motion also had an impact on vection, suggests that a simple optimally weighted sum of sensory signals is not a complete model, but that these dynamics should include influences of higher-level cognitive processes.

More recent studies have shown that, contrary to simple summation models, cognitive factors can influence perceived self-motion. For example, Wright et al. [75] conducted a study to similar to earlier vection papers [55,76] but used simulated, naturalistic visual displays that were either spatially or temporally in or out-of-phase with the motion of an oscillating seat. They found that visual scenes that were consistent with the physical surroundings tended to dominate the vestibular inputs in the perceived self-motion. They also found that oppositely directed visual and vestibular motion did not reduce or cancel out the perceived self-motion.

The role of naturalism/realism in vection has also been reported by [77] who reported that holding of an umbrella while perceiving moving stimuli as rain or snow inhibited vection. Interestingly, our finding of enhanced vection for the pipes stimuli in the upright postures—for which observers reported feeling like they were riding an elevator—provides further evidence that cognitive factors not only help shape our perceptual experience of self-motion, but may also depend on other ecological factors.

The fact that vection can be incomplete or dropout during the optic flow stimulus and produce object motion percepts are well-known phenomena [78,11,55,79]. It is possible that these differences in these cognitive effects in different postures could explain the effects we observed. In the present study, the perceived context of the visual scene varied with head orientation and motion direction relative to gravity. The resulting interpretation of the scene could have produced enhanced or inhibited vection. For instance, observers reported “flying” through the dots defining the space (i.e., the dots perceived as stars) and that this enhanced their vection experience, whereas viewing the dots as bubbles or snow falling tended to reduce their sensation of self-motion. The pipes scene was intended to produce a stronger context for a stationary environment with the expectation that this would stabilize these cognitive interpretations. With the pipes scene, observers who reported that they felt like they were riding an elevator also added that they experienced stronger vection. However, the lack of a main effect for stimulus type (i.e., dots versus pipes) but rather, an interaction of stimulus type with head orientation, suggests that both cognitive and ecological factors may be determinants in perceived self-motion.

The varied interpretations of our stimuli might be explained by the fact that, unlike in the studies by [75,6], our pipes stimulus was not a real image or virtual simulation of a naturalistic scene, but rather was more abstract. Interestingly, the interpretations of the dots stimulus varied more and seemed to influence vection both positively and

negatively, while the pipes scene provided a more consistent and positive effect on vection. We predicted and found that the rigid pipe structure—which consisted of geometric objects and frame-like structures—might be more comparable to real scenes. Observer reports seemed to indicate to greater sense of presence and enhanced vection with the pipe stimulus. Notably, most of our observers in their debrief reports related their experience of the pipes stimulus to that of riding in an elevator. It is possible that this elevator interpretation was due to expectations of being upright based on everyday experiences with elevators (despite the fact that the scenario was similar to riding in a glass elevator rather than the more commonly experienced enclosed elevator). These expectations might partially explain the increased influence of spinal orientation on vection for the pipes stimulus. Furthermore, lying on the side places pressure on the side of body and therefore may not only be less comfortable than being postured upright, but could also draw further attention to the unnatural condition and percept of riding an elevator while roll-tilted. Thus, the significant interaction between the scene and body orientation seems to indicate both higher-order cognitive processes and ecological factors in the perception of self-motion.

5.5. Summary and conclusions

Here, we have demonstrated that the perception of self-motion can be influenced by the alignment of visual motion with gravity and the body, and is also dependent on the perceived context of the scene. In Experiments 1 and 2, aligning the direction of visual motion with the gravitational vertical in upright observers resulted in vection enhancement. Yet, in postures in which the visual motion was orthogonal to the gravity vector, observers experienced stronger vection when motion was along their spinal axis, suggesting that the preference for the vertical direction may be based more on the trunk of the body or a head-based coordinate system, rather than the orientation of the body relative to gravity. The illusory self-motion also depended on the perceived context of the visual scene, which was found to be influenced by posture. Finally, when we changed the structure of the visual scene, this too impacted their experience of self-motion. Taken together, these findings support earlier findings that gravity, body orientation, and cognitive (“top-down”) processes are involved in the perception of self-motion.

Conflict of interest

We wish to confirm that there are no known conflicts of interest associated with this publication.

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